

Gerbillurus vallinus.

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Gerbillurus Shortridge, 1942

Gerbillus Desmarest, 1804:397.

Gerbillurus Shortridge, 1942:52. Type species *Gerbillus* (*Gerbillurus*) *vallinus* Shortridge, by subsequent designation (Davis, 1975).

CONTEXT AND CONTENT. Order Rodentia, Family Muridae, Subfamily Gerbillinae, Tribe Taterillini, Subtribe Gerbillurina, Genus *Gerbillurus*. Four species are usually recognized (Meester et al., 1986; Schlitter et al., 1984; Skinner and Smithers, 1990), although a fifth may be present (Davis, 1975; de Graaff, 1981). A key to the species of *Gerbillurus* adapted from Meester et al. (1986) follows:

1. Bullae normally inflated, not extending behind the occiput, up to ca. 9 mm long; tail <20% longer than head and body (Subgenus *Progerbillurus*) *G. paeba*
Bullae more inflated, extending behind occiput, >9 mm long; tail >20% longer than head and body 2
2. Bullae inflated, ca. 9–10 mm long; posterior palatal foramina very short; tail ca. 30% longer than head and body, tip of tail slightly or moderately tufted (Subgenus *Paratatera*) *G. tytonis*
Bullae inflated, ca. 10–12 mm long; posterior palatal foramina long, ca. length of molar tooth row; tail ca. 20% or 40% longer than head and body; tip of tail moderately to well tufted (Subgenus *Gerbillurus*) 3
3. Bullae inflated, ca. 10–11 mm long; tail long, ca. 40% longer than length of head and body *G. vallinus*
Bullae inflated, ca. 10.5–12.5 mm; tail shorter, ca. 20% longer than length of head and body *G. setzeri*

Gerbillurus vallinus Thomas, 1918

Brush-tailed Hairy-footed Gerbil

Gerbillus vallinus Thomas, 1918:148. Type locality "Tuin, near Kenhart, Hartbees River near 29°S, 21°E, Bushmanland, northwestern Northern Cape, South Africa."

CONTEXT AND CONTENT. Context as for genus. The following two subspecies of *G. vallinus* are recognized (Meester et al., 1986):

Gerbillurus vallinus vallinus Thomas, 1918:148. Type locality "Kenhart, Northern Cape, South Africa."

Gerbillurus vallinus seeheimi Lundholm, 1955:297. Type locality "Seeheim, Fish River, southern Namibia."

DIAGNOSIS. *Gerbillurus vallinus* is distinguished from its congeners by its longer tail, ca. 40% longer than head and body (Meester et al., 1986). *G. vallinus* (Fig. 1) differs from *G. paeba* and *G. tytonis* by its larger size and more pronounced tassel at the tip of the tail. Soles of hind feet of *G. vallinus* are naked from heel to the middle of the sole, whereas hind feet of *G. paeba* and *G. tytonis* are fully furred except for a narrow central patch (de Graaff, 1981). *G. vallinus* is dorsally darker in color than *G. setzeri* (Schlitter, 1973). Skulls of *G. vallinus* (Fig. 2) are shorter and narrower than those of *G. setzeri*, but longer and broader than those of *G. paeba* and *G. tytonis*. Auditory bullae of *G. vallinus* are less inflated than those of *G. setzeri*, but more inflated than those of *G. paeba* or *G. tytonis* (Schlitter, 1973).

GENERAL CHARACTERS. *Gerbillurus vallinus* is a small gerbil with a very long tufted tail. Hind feet are large with soles that are partially furred. Fur is soft and long (de Graaff, 1981).

Upper parts of the body vary in color from reddish-brown to dark grayish-brown with white underparts, forelimbs, and feet (Skinner and Smithers, 1990). Tail brush is deep red to black, with a dorsal tail stripe extending at least half-way up the tail (Griffin, 1990). Off-white markings above the eye and at the base and behind the ear vary in intensity and are not always discernible (Skinner and Smithers, 1990).

Mean (and range) of body mass (in g) of seven individuals collected in Namibia and northwestern Northern Cape province is 34.7 (30.0–43.0). Mean and range of external measurements (in mm) of 16 individuals are as follows: length of head and body, 96 (58–109); length of tail, 115.5 (70–145); length of hind foot, 30 (26–34); length of ear, 14 (12–15—de Graaff, 1981). Mean (and range) of external measurements (in mm) of a different collection of animals are the following: total length, 239.9 (215–266, $n = 26$); tail length, 138.9 (119–156, $n = 26$); length of hind foot, 31.2 (30–34, $n = 27$); length of ear from notch, 14.4 (14–16, $n = 27$ —Schlitter, 1973). Mean (and range) of cranial measurements (in mm) are the following: occipitonasal length, 29.9 (28.2–31.9, $n = 31$); breadth across zygomatic arches, 15.7 (15.1–16.8, $n = 32$); greatest breadth of braincase, 14.2 (13.0–15.0, $n = 29$); least interorbital breadth, 5.8 (5.4–6.3, $n = 34$); breadth of rostrum, 3.9 (3.5–4.2, $n = 33$); greatest length of nasals, 11.3 (10.3–12.4, $n = 34$); oblique length of auditory portion of auditory bulla, 10.6 (9.9–11.0, $n = 34$); crown length of maxillary toothrow, 4.1 (3.7–4.5, $n = 33$); breadth of palate at M3, 5.4 (4.7–6.5, $n = 32$); length of anterior palatal foramina, 5.2 (4.7–5.7, $n = 34$); length of posterior palatal foramina 2.0 (1.4–2.5, $n = 34$); greatest height of skull, 12.7 (11.9–13.2, $n = 25$); and breadth of auditory bulla, 8.6 (8.0–9.0, $n = 34$ —Schlitter, 1973). No sexual dimorphism is present (Schlitter, 1973).

DISTRIBUTION. *Gerbillurus vallinus* is confined to the western sector of the South West Arid Zone (Fig. 3), from Kenhardt and Tsee Rivieren in the northwestern region of the Northern Cape (Meester et al., 1986) to around Solitaire on the southeastern edge of the central Namib Desert (Griffin, 1990). An isolated population of *G. v. seeheimi* occurs on the Tsondeb River floodplain, Namibia (Griffin, 1990). Many specimens have been collected from the Brukkaros volcano area, Namibia (Griffin, 1990). Several authors (de Graaff, 1981; Meester et al., 1986) describe the distribution of *G. vallinus* as extending northwards from Swakopmund to southwestern Angola. *G. setzeri* was first described in 1973 (Schlitter, 1973); therefore previously described distribution limits for *G. vallinus* include specimens now referable to *G. setzeri*. Despite extensive trapping over 13 years, Griffin (1990) has never caught *G. vallinus* north of the Tsondeb River in Namibia. Previous records of *G. vallinus* from Central and Northern Namib, Damaraland, Kao-

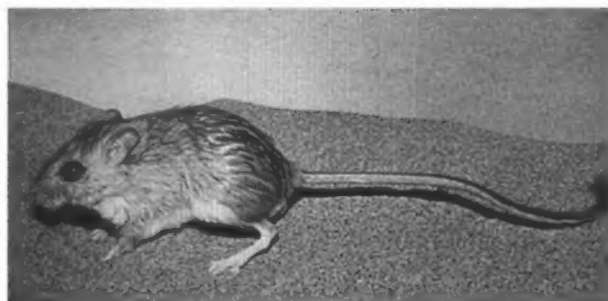


FIG. 1. *Gerbillurus vallinus*. Photograph by A. Bruton.

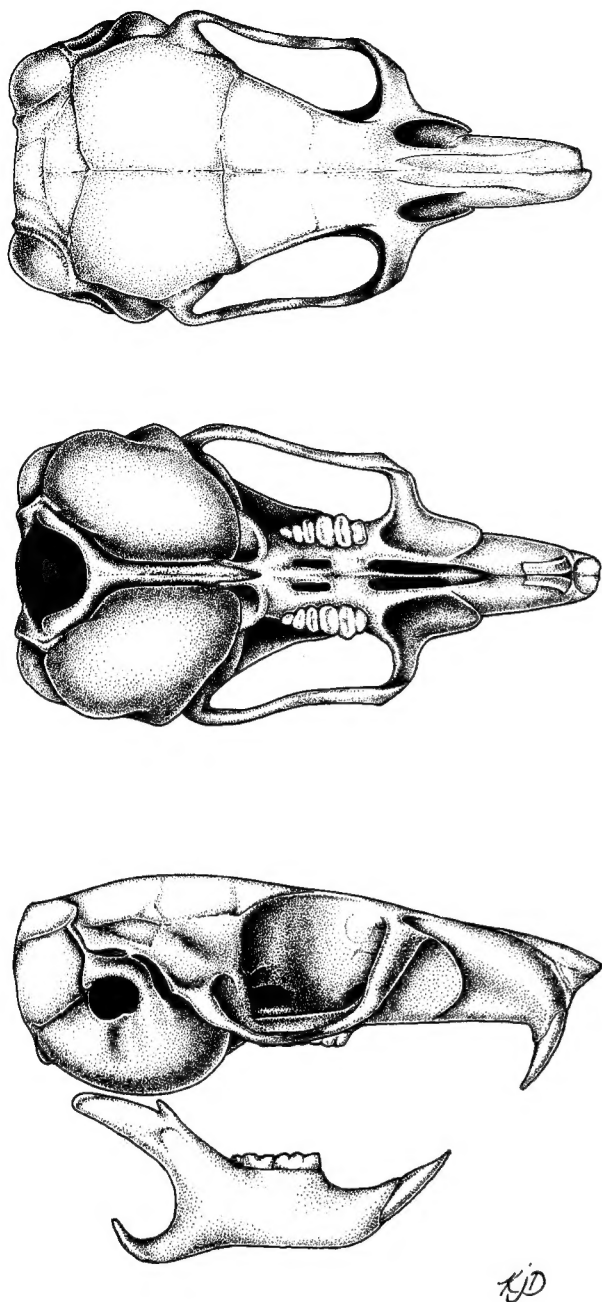


FIG. 2. Dorsal, ventral, and lateral views of the cranium and lateral view of the mandible of *Gerbillurus vallonius*. Greatest length of skull is 29.5 mm.

koland, and Angola (Crawford-Cabral, 1986) almost certainly refer to *G. setzeri*. The disjunction at the Tsondeb River is apparently the northern range limit for *G. vallonius* and the southern range limit of *G. setzeri* (Griffin, 1990). No fossils of this species are known.

FORM AND FUNCTION. Dental formula is $i\ 1/1, c\ 0/0, p\ 0/0, m\ 3/3$, total 16 teeth. *Gerbillurus vallonius* exhibits non-shivering thermogenesis but neither low temperatures nor deprivation of food induces torpor (Downs and Perrin, 1991a). At 10°C *G. vallonius* occasionally shivers, while at ambient temperatures $<20^{\circ}\text{C}$ it lies in a crouched position. Above 20°C individuals lie prostrate, but at $>35^{\circ}\text{C}$ they salivate, wetting the neck region, and show vasodilation, especially in toes, ears, and tails. Sandbathing and piloerection may also occur at high temperatures (Downs and Perrin, 1990a).

Thermal parameters are the following: thermoneutral zone, $33.1\text{--}35.0^{\circ}\text{C}$; predicted lower critical temperature, 18.6°C ; basal

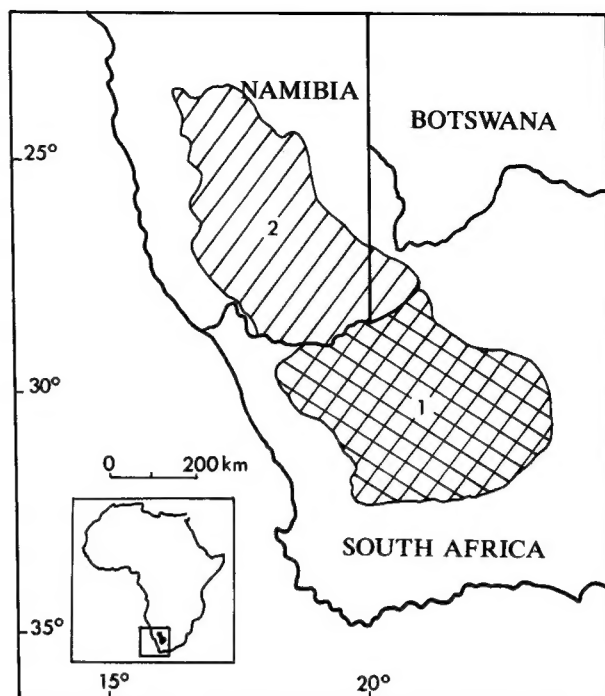


FIG. 3. Distribution of *Gerbillurus vallonius* in southern Africa. Subspecies are as follows: 1, *G. v. vallonius*; 2, *G. v. seeheimi*.

metabolic rate, $0.896\text{ ml O}_2\text{ g}^{-1}\text{ h}^{-1}$; minimal conductance, $0.13\text{ ml O}_2\text{ g}^{-1}\text{ h}^{-1}\text{ }^{\circ}\text{C}^{-1}$. Pulmocutaneous water loss is low at $<35^{\circ}\text{C}$ but increases sharply thereafter, when animals become hyperthermic and salivate. The relatively large body size of *G. vallonius* reduces the difference between total water loss and metabolic production, thereby reducing the role of metabolism in water budgets (Downs and Perrin, 1990a). Above the thermoneutral zone, *G. vallonius* shows a sharper increase in thermal conductance and a lower relative rate of oxygen consumption than the two dune species, *G. paebe* and *G. tytonis*. This may reflect an avoidance of evaporative water loss in order to reduce overheating. Although heating rate constants of *Gerbillurus* species are similar (Downs and Perrin, 1990a), the two species found on gravel plains (*G. setzeri* and *G. vallonius*) are larger and have thicker pelages (Schlitter et al., 1984), thus facilitating a greater change in thermal conductance than for dune species. Below 30°C , thermal conductance values are particularly low in *G. vallonius*.

Water turnover rate of *G. vallonius* in the laboratory varies with diet (Downs and Perrin, 1990b). On diets of sunflower seeds, millet seeds, or mealworms (each supplemented with carrots), water turnover rates are 103.5, 173.4, and $225.5\text{ ml kg}^{-1}\text{ day}^{-1}$, respectively, while mean urine production (ml/day) and mean urine concentration (osmol/kg) are 0.29, 0.89, and 0.46, and 3.70, 1.94, and 2.03, respectively (Downs and Perrin, 1990b). Urea concentrations (mMol/ml) of *G. vallonius* on sunflower seed or mealworm diets (supplemented with carrot) were 2.363 and 2.897, respectively, while allantoin concentrations are higher than for any other member of the genus (Downs and Perrin, 1991b). Like other *Gerbillurus* species, *G. vallonius* shows a high water turnover rate but good urine concentrating abilities that allow versatility in water turnover rate, depending on the protein content and potential water yield of the diet. Insect diets or supplements of succulent plant material, are important for the maintenance of water balance (Downs and Perrin, 1990b).

Gerbillurus vallonius has a simple, unilobular kidney with an elongated papilla renalis extending into the ureter (Downs and Perrin, 1991b). The renal pelvis is type II (Schmidt-Nielsen, 1977) with fornices, and it penetrates the outer medulla, indicative of an efficient urinary concentrating ability. Urine osmolalities determined in the laboratory approximate values predicted from renal anatomy (Goyal et al., 1988).

ONTOGENY AND REPRODUCTION. Studies of two captive *G. vallonius* (three estrous cycles) suggest a cycle length of

11.3 days. Presence of corpora lutea in the ovaries of two unmated females and results of vaginal smears suggest *G. vallisus* is a spontaneous ovulator (Dempster and Perrin, 1989a).

In five *G. vallisus* litters born and raised in captivity, litter size varied from 1 to 5, and neonates had a mean individual mass of 2.0 g at birth (Dempster and Perrin, 1991b). Roberts (1951) recorded a female with five young in a chamber in a burrow system. The chamber was lined with dry vegetable debris to form a nest. Young are born hairless, with eyes closed, digits fused, and ear pinnae folded down and fused to head. Incisors emerge at 11–12 days and eyes open at 16–20 days. Growth rate of 0.4 g/day was recorded for the first 23 days of life. Young are weaned at 23–28 days, when they emerge from the nest and exhibit full adult behavior patterns of locomotion, feeding, and self-grooming. Nipple-clinging does not occur (Dempster and Perrin, 1991b).

ECOLOGY. Insect exoskeletons, monocotyledon leaves, and seeds were found in burrows of *G. vallisus* at Kenhardt (Downs and Perrin, 1989). Burrows penetrate superficial soils to the underlying gravels, are ca. 6–9 cm in diameter, and possess branches or escape burrows. Burrows are more complex than those of sand dune species, *G. paeba* and *G. tytonis*. Burrows were located where mounds were formed under *Phaeoptilum spinosum* bushes; 75% of the burrows (mean depth = 267 mm) were complex with several side branches (Downs and Perrin, 1989). At a depth of 200 mm, mean burrow temperature was 29.0°C (range, 25.3–35.2) in November, relative to mean monthly minimum and maximum ambient temperatures of 13.8 and 32.9°C, respectively, and 21.6°C (19.5–24.0) in June, relative to mean monthly minimum and maximum ambient temperatures of 11.9 and 28.0°C, respectively (Downs and Perrin, 1989).

Gerbillurus vallisus is sympatric with *G. paeba* throughout most of its range. In the central part of its distribution, at Brukkaros-Berseba in Namibia, *G. vallisus* is numerically more abundant than *G. paeba* (Griffin, 1990). However, at the limit of its distribution in the Tsondab valley the situation is reversed.

BEHAVIOR. *Gerbillurus vallisus* is gregarious, terrestrial, and nocturnal (Skinner and Smithers, 1990). Locomotion is saltatorial but quadrupedal (Dempster and Perrin, 1990c). In staged male-female encounters, male *G. vallisus* followed, sniffed the female's anogenital region, and mounted females significantly more frequently than females followed, sniffed, or mounted males. Females retreated from males more frequently than males retreated from females. *G. vallisus* exhibited more huddling and less upright and submissive behavior, and females exhibited less upright and aggressive behavior than other *Gerbillurus* species (Dempster et al., 1992). Thus, *G. vallisus* are less aggressive than other *Gerbillurus* (Dempster and Perrin, 1989b, 1989c) and may be a tolerant or semi-social species, a finding that is supported by the complexity of burrows (Downs and Perrin, 1989).

Like other *Gerbillurus* species, *G. vallisus* scatter-hoards food in the laboratory, sandbathes using side-flicking and side-rubbing, constructs nests of shredded grass and seed husks, and communicates using foot drumming. *G. vallisus* digs with its forepaws and then kicks the sand backwards with its hind feet. The most common sleeping posture is a curled position, with head tucked under the body and tail curled around the feet (Dempster and Perrin, 1990).

Ultrasonic calling by *G. vallisus* is by means of strongly modulated frequency sweep calls with a frequency range of 40–22 kHz and a mean duration of 55 msec (Dempster and Perrin, 1991a). *G. vallisus* also produces a long modulated whistle in the audible range at ca. 12 kHz. Vocalizations occur significantly more frequently than expected during sexual and huddling behavior, and following mutual investigation and aggressive behavior. Vocalizations seldom accompany upright or submissive behavior (Dempster et al., 1991).

GENETICS. Based on the standard karyotypes of 13 individuals, *Gerbillurus vallisus* has a diploid number of 60 with 80 autosomal arms (Schlitter et al., 1984). Autosomes include 5 pairs of metacentrics, 6 pairs of submetacentrics, and 18 pairs of acrocentrics. The X chromosome is the largest chromosome, whereas the Y chromosome is a small acrocentric chromosome (Schlitter et al., 1984). Intraspecific variation in the number of autosomal arms from 70 to 74 was reported for five specimens of *G. vallisus*. Individuals varied in the number of heterochromatic short arm ad-

ditions to chromosomes 1 and 8 (Qumsiyeh, 1986; Qumsiyeh et al., 1991).

Within the genus *Gerbillurus*, the karyotype of *G. vallisus* is most similar to that of *G. setzeri* (Qumsiyeh et al., 1991). The two species share seven centric fissions and two translocations. *G. vallisus* has the following unique derived conditions: centric fissions in 7/8, 19/20, 25/26 and translocations involving 11/12 and 29. Other differences between *G. vallisus* and *G. setzeri* occur as polymorphisms (Qumsiyeh et al., 1991).

REMARKS. The generic name *Gerbillurus* is derived from the French *gerbille* meaning "a small rodent". The suffix *urus* denotes "as belonging to". The species name *vallisus* comes from the Latin word *vallis*, "a valley". The name *G. vallisus* therefore implies a small rodent inhabiting valleys (de Graaff, 1981).

Gerbillurus was originally described as a subgenus of *Gerbillus* to differentiate the "paeba" group (subgenus *Gerbillus*) from the "vallisus" group (subgenus *Gerbillurus*—Shortridge, 1942). *Gerbillurus* was raised to generic status by Roberts (1951), which was supported by Lundholm (1955), whereas *Gerbillus* was retained as a separate genus for the "paeba" group of southern African pygmy gerbils. Southern African pygmy gerbils were assigned to the genus *Gerbillurus*, retaining the genus *Gerbillus* only for north African gerbil species (Petter, 1975). Davis (1975) was not convinced that the southern African pygmy gerbils should be separated generically from the north African *Gerbillus* species, nor that *Gerbillurus paeba* and *G. vallisus* belong to the same genus. Subsequent authors (de Graaff, 1981; Meester et al., 1986; Smithers, 1984) retained *Gerbillurus* as a valid genus. Cranial characteristics support separation of *Gerbillurus* from *Gerbillus* (Pavlinov, 1982). *Gerbillurus* species lack median crest connections between molar laminae in upper and lower jaws, whereas *Gerbillus* species have such connections (Davis, 1975). In addition, *Gerbillurus* species have well-haired or fairly well-haired soles of the hind feet; cusps of molar laminae in upper and lower jaws that are less alternate in position than in *Gerbillus* species; and alveolar patterns in m1 with four sockets, in M1 with three or four sockets, and in M2 mostly with three sockets (Davis, 1975). *Gerbillurus* is more "Tatera"-like than *Gerbillus* species (Herold and Niethammer, 1963). Evidence from karyological and craniological studies confirm that the genus *Gerbillurus* is monophyletic (Pavlinov, 1987; Qumsiyeh et al., 1991; Schlitter et al., 1984).

Two subgenera were recognized by Pavlinov (1982): subgenus *Gerbillurus* included the specialized species endemic to the Namib Desert, while subgenus *Progerbillurus* included the most widespread and primitive species, *G. paeba*. Further analysis of teeth and tympanic bullae of *Gerbillurus* species led Petter (1983) to propose a new subgenus, *Paratatera*, for *G. tytonis*. *Paratatera* resembles *Progerbillurus* in the size of the tympanic bullae, but it has very short posterior palatal foramina, unlike species of the subgenera *Gerbillurus* and *Progerbillurus*. Subsequently, Pavlinov (1987) suggested that subgenera *Gerbillurus* and *Paratatera* should be regarded as "species groups" within one subgenus, *Gerbillurus*, and that *Progerbillurus* should be retained as a separate subgenus. Skull drawings were done by K. Duxbury.

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